BREEDING BIOLOGY OF THE MALABAR GREY HORNBILL (OCYCEROS GRISEUS) IN SOUTHERN WESTERN GHATS, INDIA.¹

DIVYA MUDAPPA²

(With one text-figure)

Key words: hornbill, tropical rainforest, frugivory, seed dispersal, cavitynesting, breeding biology

The Malabar grey hornbill (Ocyceros griseus) is a frugivore, endemic to the tropical rainforests and moist deciduous forests of the Western Ghats hill ranges, India. I studied its breeding biology in the Anamalai hills (Indira Gandhi Wildlife Sanctuary), Tamil Nadu state, by monitoring 10 nests and their middens, and conducting intensive observations at a focal nest. The nesting period lasted an average of 86 days (N=4), and observations at the focal nest revealed the pre- and post-hatching phases to be 40 and 46 days, respectively. At the end of the nesting period, the females and the young simultaneously broke out of the nests. A total of 2397 items of food were delivered by the male hornbill to the inmates of the focal nest. They included 6 species of lipid-rich and 8 species of sugar-rich fruits, and at least 14 kinds of animal matter. Lipid-rich fruits formed a major component (c. 37%) of the diet during nesting. Ficus fruits formed 26%, and animal matter 13.8% of the diet of the incarcerated hornbills. The frequency of sugar- and lipid-rich fruits delivered per hour of observation was significantly greater in the pre-hatching phase. While the frequency of animal food delivered was higher in the post-hatching phase. Although the Malabar grey hornbill used a wide range of food resources, it was observed that a few species of rare, tropical trees producing lipid-rich fruits during the nesting period, play an important role in the maintenance of the species.

INTRODUCTION

Hornbills (Aves : Bucerotidae and Bucorvidae) are a group of large, forest and savanna birds restricted to the Old World tropics. There are 54 species of hornbills in the world (Kemp 1988, 1995), nine of which occur in India (Ali and Ripley 1987). Only in the last two decades, a few studies have provided valuable insights into the ecology of these unique cavitynesting birds (Hussain 1984, Kannan 1994, Kemp 1976, 1978, 1988, Kinnaird 1993, Leighton 1982, Poonswad 1995, Poonswad and Tsuji 1989, 1994, Reddy *et al.* 1990, Reddy and

¹Accepted June, 1998 ²Centre for Ecological Research and Conservation 3076/5 IV Cross, Gokulam Park Mysore 570 002, Karnataka, India. Basalingappa 1995). Hornbills are secondary cavity-nesters, and the forest-dwelling species are predominantly frugivorous. Their breeding cycles are synchronous with food productivity of the forest (i.e., fruiting phenology; Kannan 1994), but they are also dependent on keystone resources like *Ficus* for their survival in times of low food availability. They exhibit wide-ranging movements to meet their specialized food requirements (Poonswad 1994). Functionally, they have been described as keystone mutualists (Gilbert 1980) as they play an important role in the dispersal of many rare rainforest tree species (Kinnaird 1998, Whitney *et al.* 1998).

The present study aimed to determine the nesting habitat requirements and breeding biology of the Malabar grey hornbill, endemic to the Western Ghats. The former aspect is dealt with elsewhere (Mudappa and Kannan 1997). This paper describes in detail: 1) nesting activities and behaviour of the male and female hornbill, 2) duration of nesting period and distinct phases of the nesting cycle, and 3) qualitative and quantitative data on the food delivered by the male to the incarcerated female and young, in relation to the phases of the nesting period. The results are compared with other hornbill species, their reproduction and survival strategies, and the implications for the conservation of this rainforest endemic are discussed.

STUDY AREA

The study was undertaken between December 1993 and May 1994 at the Indira Gandhi Wildlife Sanctuary (10°13' - 10°33' N and 76°49' - 77°21' E, an area of 968 km²) in the Anamalai Hills of the southern Western Ghats, in Tamil Nadu state, India. A one-month long preliminary study was carried out in the area in May-June 1993, when 15 nests were discovered and seeds from the middens were collected and identified for future reference. The nests selected for intensive observation and monitoring were in the 5.1 km² wet evergreen' forest patch of Karian Shola National Park. This forest, classified as a Southern Tropical Wet Evergreen Forest (Champion and Seth 1968), receives an annual rainfall of about 1500 mm. The terrain is hilly, and the altitude ranges from 350 m to 2400 m above msl in the Sanctuary, which extends into Parambikulam Wildlife Sanctuary and Eravikulam National Park in the adjacent Kerala state. The forest is contiguous with moist deciduous, teak (Tectona grandis) and bamboo forests in the surrounding areas.

STUDY SPECIES

Of the 9 species of hornbills in India, the Malabar grey hornbill (*Ocyceros griseus*), is the smallest. It is endemic to the Indian subcontinent, occuring only in the heavy rainfall tracts of the Western Ghats hill ranges. Most of the information on the Malabar grey hornbill and other Indian hornbills is anecdotal with notes on natural history. Early papers dealing with nidification of the Malabar and the common grey hornbills (*Ocyceros birostris*) are those of Bingham (1879), Hall (1918), Lowther (1942), and Abdulali (1942). More comprehensive information on their ecology and behaviour was provided by Ali and Ripley (1970, 1987) and Kemp (1978).

The Malabar grey hornbill is sexually dimorphic: the male has a large, bright orange bill and golden brown iris, while the female has a relatively small and pale-coloured bill and dark brown iris. The species is monogamous, the nesting pair usually exhibiting high nest-site fidelity, occupying the same nest-cavities every year (Kemp 1978, Ali and Ripley 1987, Mudappa and Kannan 1997). The Malabar grey hornbill exhibits biparental care like most other monogamous birds with altricial young (Clutton-Brock 1991). While the incubating female is incarcerated, the male provisions her and the other inmates of the nest.

Methods

Active nests of the Malabar grey hornbill were located with the help of a local field assistant, by following the parent birds, and by checking for signs of previous nesting, such as seeds and faecal remains (midden) at the base of the nest trees. Fifteen nests were located during the preliminary study in May 1993. Seeds collected from the midden were catalogued and used for reference during the study. Twelve additional nests were discovered during the initial half of the study (December 1993 to March 1994). Ten nests were chosen for monitoring during the nesting period (the period of incarceration of the female and the young) in Karian Shola National Park. Of these, one was selected on the basis of logistics for intensive observation.

Intensive observation of a focal nest: The focal nest was observed from the last week of January 1994 to May 1994, for approximately six-hour intervals on every alternate day (more or less uniformly) throughout the three-month nesting period. Observations were made between 0700 h and 1300 h. The forenoon was chosen for nest observation, while the rest of the day was used to visit the other nine nests.

I observed the nest to gather information on the quantity and quality of food delivered by the male to the incarcerated inmates. The food was broadly classified as plant and animal food. The plant food was further categorised as: a) figs, b) sugar-rich non-fig, and c) lipid-rich fruits, based on McKey (1975) and Snow (1981). Observations were made from a ground hide about 18 m from the base of the focal nest through a 7x50 binoculars or a 20x50 spotting scope. For each visit by the male hornbill to the nest, I recorded the number and type of food items delivered, the duration of the visit (to the nearest 5 seconds), and the total number of visits during each sampling/observation session. Ad libitum observations on other activities like nest-cavity sealing, cleaning, excretion, begging by the inmates, and the behaviour of the male during the time of food delivery were recorded. At the end of each session, the seeds and other faecal remains in the midden were examined, identified, classified, and counted.

Nest midden monitoring: Ten nests (including the focal nest) were visited regularly to note the status of nesting, quantify the regurgitated or excreted seeds of the fruits eaten by the inmates, and to identify the other debris in the midden. Of the food items consumed by the nest-cavity inmates, only non-digestible parts such as seeds of fruits, elytra of insects, and reptile scales occur in the midden. All distinguishable midden remains were collected, identified, counted, and recorded. The midden below the nest-tree was cleared of all debris after each visit. Small seeds and animal matter in the faecal remains could not be quantified. The presence of Malabar grey hornbill feathers in the midden was taken to indicate moulting. Similarly, the presence of egg-shell in the midden, or the characteristic begging calls of the young, were evidence of hatching or the presence of chick(s) in the nest.

Statistical analyses: The frequency of food items delivered during the nesting period was calculated. Differences between the food (type and quantity) consumed between the two distinct phases (pre- and post-hatching) of the nesting period were tested for statistical significance using Mann-Whitney U test (Seigel and Castellan 1988), using SPSS/PC+ computer software (Norušis 1990). The difference in the occurrence of seeds (frequency) in the midden was tested for significance, using the nonparametric Mann-Whitney U Test similar to the analysis of direct feeding observation.

RESULTS

Characteristics and occupation of focal nest: The focal nest cavity was located at about 14 m on an *Artocarpus lakoocha* (Moraceae) tree. The diameter at breast height (1.2 m) of the focal nest tree was 56 cm, the height 25 m, and the estimated diameter at nest height was 50 cm. The cavity entrance was circular in shape, and oriented towards northwest. My field assistant observed a bird entering the nest cavity in the first week of February. This was probably an instance of nest preparation, cleaning, and widening of the nest entrance.

After this, there was regular movement of the breeding pair in the vicinity of the nest-tree. On February 17, the female hornbill was seen entering the nest-cavity. The cavity entrance was then half-sealed. The male and the female visited the nest (8 times in 6 hrs). During these visits, they appeared to be enlarging the cavity entrance. The female was in the nest on February 18, and was seen sealing the cavity entrance, leaving only a slit, through which the male fed the inmates during the nesting period.

The male was never observed to be involved in nest sealing, repair, or delivering any kind of sealing material, unlike the female which often repaired the seal with its bill. The female was seen cleaning the nest-cavity by throwing out a lot of seeds and woody debris. The female hornbill used her own excreta, rich in *Ficus* seeds, as material for sealing the cavity entrance. The inmates effected nest sanitation by squirting their excreta out through the slit-like opening of the cavity entrance.

Nesting period: The nesting season lasted for about three months, between February and May in the study population of the Malabar grey hornbills. The nesting period could be distinguished into two main phases: the prehatching and the post-hatching phase. However, each phase in turn has been further divided into 3 sub-phases (fortnightly) for analysis. The nesting period in the focal nest was 86 days, commencing from February 18 (incarceration of the female) to May 15 (emergence of chick and female from the nest). The mean duration of the nesting period was 86 days (\pm 2.7 S.D.; N=4).

In the focal nest, the young hatched 40 days after the incarceration of the female. The posthatching phase was 46 days. Only one chick appeared to have fledged. The female and young broke out of the nest together. Details of the nesting period in the ten nests are given in Table 1.

Clutch size and moulting: The clutch size in the breeding population could not be determined. In the focal nest, only one young was seen. One nest when examined on March 1, 1994, had only one egg. A week later, there were two eggs in this nest. The female resealed the cavity entrance and bred successfully.

Flight feathers were collected from the midden occasionally, particularly in the month of April. The rectrices were never found and the

Nest number	Date of	Fledging date		
	incarceration			
1.	17 February	16 May		
2.	15 February	3 May		
3.	18 February	13 May*		
4.	18 February	15 May*		
5.	21 February	16 May		
6.	18 February	18 April**		
7.	4 March [#]	11 May*		
8.	17 March [#]	13 May		
9.	3 March [#]	16 May		
10.	18 February	15 May		

TABLE 1 DATES OF INCARCERATION AND FLEDGING IN THE STUDY NESTS

- The chick fledged between this day and 20 May

** — Abandoned

— Nests discovered after the nesting had commenced

female of the focal nest had tail feathers throughout the nesting period. These could be seen while the bird was ejecting the faecal matter through the slit. However, rectrices had been collected from the midden of six nests during the preliminary study in 1993. Thus, it is likely that the moult in this species is partial.

Food delivery by the male hornbill: The focal nest was observed for a total of 161 hours and 45 minutes. All through the nesting period, the male provisioned the incarcerated female and later, the young also. A total of 2,397 food items, which included 11 kinds of fruit, 5 species of vertebrates, and at least 8 types of invertebrates, including 6 types of insects, were delivered by the male (Appendix). Lipid-rich fruits predominated in the diet of the incarcerated hornbills, constituting 36.9% of the food delivered. Other food categories were Ficus 26%, sugar-rich fruits 22.6%, and animal matter 13.8%. If there were several items, these were regurgitated one by one. Large fruits and vertebrate prey were usually brought as single items.

The number of food items delivered peaked during the pre-hatching phase, and declined thereafter, being minimum before the fledging of the young. The frequency of lipid-rich and

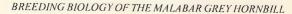
BREEDING BIOLOGY OF THE MALABAR GREY HORNBILL

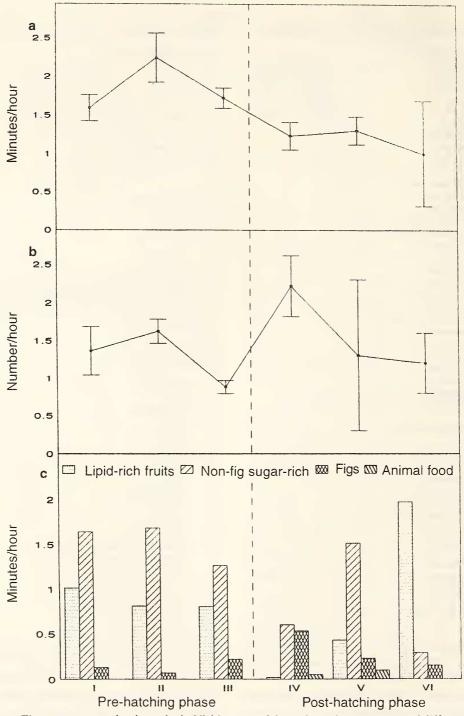
APPENDIX

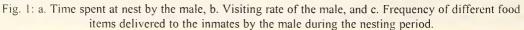
PLANT AND ANIMAL FOOD DELIVERED AT THE NEST BY THE MALE MALABAR GREY HORNBILL

A: Plant food (fruit)					A: Plant food (fruit) (contd.)					
S.No.	Species (Family)	Habit	Number in pre- hatching phase	Number in post- hatching phase	S.No.	Species (Family)	Habit	Number in pre- hatching phase	Number in post- hatching phase	
Suga	r-rich Fruit				17.	Knema attennata				
1.	Ficus spp.					(Myristicaceae)*	Tree			
	(Moraceae)	Tree/	443	123	18.	Polyalthia sp.				
		Strangler				(Annonaceae) ⁺	Trec	-	-	
2.	Mimusops elengi									
	(Sapotaceae)	Tree	17			Other Fruits				
3.	Bridelia sp.				19.	Strychnos				
	(Euphorbiaceae)	Climber	417	13		nux-vomica				
4.	Elaegnus conferta					(Loganiaceae)*	Tree		_	
	(Elaegnaceae)	Climber	4		20.	Unidentified**				
5.	Linocera				20.	Unidentified				
	intermedia					E 11 4 11	0.0 0			
	(Sapindaceae) ⁺	Tree		_	+	i conta tit tito titi da				
ó.	Syzygium spp.				*	rotaria in the initiatio				
	(Myrtaceae) ⁺	Tree		_	**	ren species milose				
7.	Filicium decipiens					in the middens (the	ree were fou	ind in the mi	dden of t	
	(Oleaceae)*	Tree		_		focal nest)				
3.	Zizvphus									
	nununularia					B: Animal Food				
	(Rhamnaceae)	Shrub	61		Vertel	orates				
).	Glycosmis									
	pentaphylla				1.	Young bird				
	(Rutaceae)	Shrub	11	_	2.	Snake				
	(**********				3.	Lizard (Calotes sp	i.)			
	Lipid-rich Fruit				4.	Gecko				
10.	Uvaria sp.				5.	Frog				
	(Annonaceae)	Climber	510	63						
11.	Neolitsea sp.	cannoer	210	05	Invert	ebrates				
	(Lauraceae)	Tree	173	52						
12.	Cinnamomum sp.	1100	175	52	1.	Beetle				
, 2.	(Lauraceae)	Tree			2.	Cricket/Grasshopp	ber			
13.	Persea macarantha				3.	Cicada				
	(Lauraceae)*	Tree	1000	_	4.	Stick Insect				
14.	Litsea sp.	1100			5.	Caterpillars				
, 4.	(Lauraceae) ⁺	Tree			6.	Winged insect (wa		etc.)		
15.	(Lauraceae) Beilschmedia sp.	ince			7.	Millipede/Centipe	de			
19.	(Lauraceae)	Tree		19	8.	Scorpions				
16.	(Latitaceae) Myristica	nee		19						
10.	~				Total	number of animal fo	od items de	livered durin	g the	
	dactyloides	Trees			10141	nesting period			ethe	
	(Myristicaceae)*	Tree	- And			neoting period				

non-fig sugar-rich fruits was significantly higher in the pre-hatching phases (Mann-Whitney U test, N=16, U=24, p<0.001 and U=36, p<0.001, respectively). Figs were eaten consistently throughout the nesting period. The frequency (number per hour of observation) of animal matter delivered was greater in the post-hatching phase (Mann-Whitney U test, U=41, p=0.047 for invertebrates and U=64, p=0.014 for vertebrates; Fig. 1). Within the pre-hatching phase, the frequency of lipid-rich fruits was significantly higher than the other types (Kruskal-Wallis







 χ^2 =13.48, df=3, p<0.001), while in the posthatching phase, animal food was significantly greater (χ^2 =23.26, df=3, p<0.001).

Time spent at nest and visitation rate of the male: The time spent and the visitation rate of the male hornbill was influenced by the number and type of items delivered. Time spent (minutes per hour of observation) was significantly higher (Mann-Whitney U test, U=38, p<0.01) in the pre-hatching than in the post-hatching phase, as a greater number (69.5%) of small fruits (≤ 1.5 cm) was delivered (each had to be regurgitated individually). The visitation rate did not differ between the phases (Fig. 1).

Feeding habits — evidence from middens: Supplementary data from the middens of the ten nests showed that nine additional species of fruits were consumed by the incarcerated hornbills (e.g. *Strychnos nuxvomica, Litsea* sp., *Persea macarantha*, see Appendix). A few seeds of ten unidentified plant species were collected from some middens. There was no significant difference between the preand post-hatching phases in the frequency of the lipid-rich fruit seeds collected in the midden. The frequency of non-fig sugar-rich fruit seeds in the midden was found to be significantly greater in the pre-hatching phase (Mann-Whitney U test, N=21, U=116, p=0.007).

Predation on Malabar grey hornbill and nest intrusion: Two cases of mortality of Malabar grey hornbills were recorded. The first was of a young bird found towards the end of the nesting period during the preliminary study in 1993. The second was presumably an adult, whose remains were found in the middle of the nesting period in 1994, close to a regularly monitored nest which had been abandoned five days earlier.

The focal nest was once visited by three hill mynas (*Gracula religiosa*) that flew away at the approach of the male hornbill. A Malabar giant squirrel (*Ratufa indica*) and the duskystriped palm squirrel (*Funambulus sublineatus*) were other inquisitive visitors to the nest, but were apparently disregarded by the incarcerated female.

DISCUSSION

The 32 species of Oriental hornbills are essentially forest-dwelling, arboreal birds (Kemp 1988, 1995). These species, including the Malabar grey hornbill, are long-lived, and have a distinct and relatively long nesting period. The nesting period of the Malabar grey hornbill lasted an average of 86 (\pm 2.7 days) during this study. The success of this bird as a rainforest specialist can be attributed to its life-history strategies (the long and peculiar nesting behaviour), and the adaptation in food habits.

Predation of adult Malabar grey hornbills by animals other than man is rare. Even during the vulnerable period of incarceration, the chances of predation are low, because the nestcavity entrance is sealed, and the female with her large, armoured bill can protect the nest from intruders. This protection, along with the cavity nesting habit, can be the reason for the long incubation period of these birds.

Overall, the nesting period and food delivery by the Malabar grey hornbill in the area, as in the case of great pied hornbill (Buceros bicornis), seems to be associated with fruiting phenology, and the onset of the southwest monsoon (Kannan 1994). Studies in Thailand (Poonswad et al. 1988) have found the nesting of hornbills to commence and terminate later than in this region, probably because of the later monsoon. Hornbills subsist on an array of diverse, locally rare, tree species (e.g. members of the Lauraceae; Kannan and James 1999). The nesting period coincides with the peak in fruit availability, as shown by the fruiting phenology study of Kannan and James (1999). Large numbers of rainforest trees of the families Lauraceae, Burseraceae, and Myristicaceae (op cit.) contribute to the abundance of fruit.

BREEDING BIOLOGY OF THE MALABAR GREY HORNBILL

Lipid-rich fruits formed the most abundant component of the food delivered. The coincidence of nesting with peak in lipid-rich fruit availability could be as a result of long-term co-evolutionary process (McKey 1975). The high lipid content of these fruits may be necessary to meet the requirements of the nesting, moulting, and growing birds (Snow 1981).

Protein, carbohydrate, and water is obtained from sugar-rich fruits (including figs) and animal matter, which supplement the lipidrich diet of the nesting hornbills. Notably, the Malabar grey hornbill fed less on *Ficus* fruits (26%) than the great pied, oriental pied (*Anthracoceros coronatus*), and wreathed (*Aceros undulatus*) hornbills (Kannan and James 1997, Tsuji 1996). The smaller white-throated brown hornbill (*Ptilolaemus tickelli*), however, is shown to feed less on figs.

Smaller-sized hornbills are able to feed on a wider range of fruit and animal food, probably due to their smaller body size which enables them to access even the understorey shrub species, thus reducing the predominance of any one type of food. The Malabar grey hornbill consumes a greater variety of sugar-rich, particularly understorey fruits, as well as fruits of small trees and climbers, unlike the larger syntopic great pied hornbill which prefers large, canopy and emergent trees (Kannan 1994).

A wide range of food items are fed to the nest inmates. The kind of food delivered influenced the visitation rate, and the time spent at nest by the male. The time spent was significantly higher in the pre-hatching phase as there was a greater number of small fruits (both lipid- and sugar-rich fruits, i.e., 61% of all small fruits) delivered at the nest. The time spent at the nest decreased towards the end of the nesting period, when large fruits and animal food were brought for the inmates and delivered as a single item per visit. The visitation rate did not differ between the phases, though the number of fruits delivered per visit decreased in the post-hatching phase. This was probably compensated by the nutritive quality (lipid-rich fruits and animal food), and larger size of the food items delivered (eg. fruits of *Myristica* sp., *Beilschmedia* spp.). There was a drastic fall in the number of visits during the last few days of the nesting period. Welty (1982) proposed that the steady decline in feeding frequency may be a naturally evolved strategy of the parent to encourage the nearlyfledged young to leave the nest.

The differences in the food delivered during the nesting period can be explained by one or a combination of the following factors: (i) It could be related to the availability of fruits due to the usually high seasonal and synchronous fruiting of tree species bearing lipid-rich fruits (Snow 1981, Leighton and Leighton 1983, Kannan and James 1999), while the sugar-rich fruits are available all through the year. Community fruiting patterns in the study area were found to be largely determined by the trees producing lipid-rich fruits like Lauraceae, Annonaceae, which form a major proportion of tree species in the area (Kannan 1994). It was observed that certain fruits such as Alseodaphne semecarpifolia, Litsea sp., and Persea macarantha, which were common and abundant in the middens during the preliminary study in 1993, were absent in 1994. So, inter-annual differences in fruiting patterns, and intraseasonal staggering in the fruiting patterns of the Lauraceae in the rainforests is likely to play a major role in the nesting and nesting success of the hornbills (Snow 1981, Leighton 1982, Leighton and Leighton 1983, Kannan and James 1999).

(ii) Another possibility is that the hornbill selects high quality nutritive food for the growing chicks in the post-hatching phase, feeding them largely lipid-rich fruits and animal matter, which may be of co-evolutionary significance. The increased delivery of animal food toward the end of the nesting season may reflect an increase in abundance of insect prey in the forest just after the rains. The supplementation of high quality animal matter, however, coincides with the hatching of the chick and may provide the growing chick with essential nutrients.

(iii) Hornbills are known to be territorial, ranging between 3 to 30 km² (white-throated brown and great pied hornbills, respectively) depending on the size of the bird (Poonswad and Tsuji 1994). Seeds of some fruits (eg. *Filicium decipiens*, *Polyalthia* sp.) were found in the middens of only a few nests, probably because these fruiting trees were abundant in the territories of the hornbills inhabiting those nests.

CONCLUSION

The Western Ghats have been identified as one of the biodiversity hotspots in the world (Myers 1990, 1991). However, large scale deforestation for dam construction, agriculture and other developmental activities has resulted in the loss of over 40% forest cover in the last 70 years (Chattopadhyay 1985, Menon and Bawa 1997). This in turn has restricted the range of many species, including many endemics such as

- ABDULALI, H. (1942): The nesting of the Malabar Grey Hornbill. J. Bombay nat. Hist. Soc. 43:102-103.
- ALI, S. & S. D. RIPLEY. (1970): Handbook of the birds of India and Pakistan. Vol 4. Oxford University Press. Pp. 130-133.
- ALI, S. & S. D. RIPLEY. (1987): Compact handbook of the birds of India and Pakistan. Oxford University Press, Delhi.
- BINGHAM, C. T. (1879) Notes on the nidification of some hornbills. *Stray Feathers* 8:459-463.
- CHATTOPADHYAY, S. (1985): Deforestation in parts of Western Ghats region (Kerala), India. J. Environ. Manage. 20:219-230.
- CHAMPION, H. G. & S. K. SETH (1968): A Revised Survey of the Forest types of India. Manager of Publications, Government of India, New Delhi.
- CLUTTON-BROCK, T. H. (1991): The evolution of parental care. Princeton University Press, Princeton.
- GILBERT, L. E. (1980): Food-web organization and the

the Malabar grey hornbill. Hornbills play an important role in the dynamics of their habitats because of their specialised frugivorous habits (McKey 1975, Snow 1981, Leighton 1982) and as effective dispersers of many tree species (Kinnaird 1998, Whitney *et al.* 1998).

The Malabar grey hornbill, like other members of the family Bucerotidae, act as keystone species in the range of its distribution (Gilbert 1980). This endemic, specialist frugivore of the rainforest of the Western Ghats plays an important role in the dynamics of the moist evergreen forest it inhabits, dispersing the seeds of a few rare rainforest tree species. Conservation of their habitat is imperative as they have specialised feeding and nesting requirements (Mudappa and Kannan 1997).

ACKNOWLEDGEMENTS

The research was supported by a grant from the Oriental Bird Club, U. K. I thank R. Kannan for guidance and encouragement and Ganesh, my assistant, for help in field work. I thank the Tamil Nadu Forest Department for permission to carry out the study.

REFERENCES

conservation of neotropical diversity. Pp. 11-34. *In* Soulé M. E. and Wilcox, B. A. (eds.). Conservation Biology, Sinauer, Sunderland, Massachusetts.

- HALL, E. F. (1918): Notes on the nidification of the Common Grey Hornbill (Lophoceros birostris). J. Bombay nat. Hist. Soc. 25:503-505.
- HUSSAIN, S. A. (1984): Some aspects of the biology and ecology of Narcondam Hornbill (*Rhyticeros* narcondami). J. Bombay nat. Hist. Soc. 81:1-18.
- KANNAN, R. (1994): Ecology and conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of southern India. Unpubl. Ph. D. thesis, University of Arkansas, Arkansas.
- KANNAN, R. & D. A. JAMES (1997): Breeding biology of the great pied hornbill (*Buceros bicornis*) in the Anamalai hills of southern India. J. Bombay nat. Hist. Soc. 94: 451-465.
- KANNAN, R. & D.A. JAMES (1999): Fruiting phenology and the conservation of the great pied hornbill (*Buceros*)

bicornis) in the Western Ghats of Southern India. *Biotropica 31*: 167-177.

- KEMP, A. C. (1976): A study of the ecology, behaviour and systematics of *Tockus* hornbills (Aves: Bucerotidae). *The Transvaal Mus. Memoir 20.*
- KEMP, A. C. (1978): A review of the hornbills: biology and radiation. *The Living Bird* 17:105-136.
- KEMP, A. C. (1988): The systematics and zoogeography of Oriental and Australasian hornbills (Aves: Bucerotidae). Boun. zool. Beitr. 39:315-345.
- KEMP, A.C. (1995): The hornbills. Ox ford University Press. Ox ford, England
- KEMP, A. C. & M. I. KEMP (1975): Report on a study of hornbills in Sarawak, with comments on their conservation. World Wildlife Fund Project Report 2/ 74.
- KINNAIRD, M. F. (1993): Variation in fruit resources and the effects on vertebrate frugivores: the role of disturbance regimes in Sulawesi rainforests. Report, LIPI. Jakarta, Indonesia.
- KINNAIRD, M. F. (1998): Evidence for effective seed dispersal by the Sulawesi red-knobbed hornbill *Aceros cassidix. Biotropica* 30: 50-55.
- LEIGHTON, M. (1982): Fruit resource and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Unpubl. Ph. D. thesis, University of California, Davis.
- LEIGHTON, M. & D. R. LEIGHTON (1983): Vertebrate responses to fruiting seasonality within a Bornean rainforest. pp 181-196. *In*: Sutton, S. L., Whitmore, T. C., and Chadwick, A. C. (eds.) Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications, Oxford
- LOWTHER, E. H. N. (1942): Notes on some Indian birds. J. Bombay nat. Hist. Soc. 43:386-401.
- McKEY, D. (1975): The ecology of coevolved seed-dispersal system. Pp. 159-199. *In* Gilbert L. E. and P. H. Raven (eds.). Coevolution of animals and plants. University of Texas Press, Austin.
- MENON, S. & K. S. BAWA (1997): Applications of geographical information systems, approach to biodiversity conservation in the Western Ghats. *Curr. Sci.* 73: 134-145.
- MUDAPPA, D. (1994): Nesting habitat of the Malabar Grey Hornbill (*Ocyceros griseus*) in the Anaimalais, southern Western Ghats, India. M. S. dissertation, Sálim Ali School of Ecology, Pondicherry University, Pondicherry.

- MUDAPPA, D. & R. KANNAN (1997): Nest-site selection by the Malabar Grey Hornbill (*Ocyceros griseus*) in southern Western Ghats, India. *Wilson Bull.* 102:111-119.
- MYERS, N. (1990): The biodiversity challenge: expanded hot-spots analysis. *Environmentalist 10:* 243-256.
- MYERS, N. (1991): Tropical forests: present status and future outlook. *Clim. Change 19:* 3-12.
- NORUŠIS, M. J. (1990): SPSS/PC+: Statistics 4.0. SPSS Inc., Chicago.
- POONSWAD, P. (1995): Nest-site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis 137*: 183-191.
- POONSWAD, P. & A. TSUJI (1989): Conservation of hornbills in Thailand. Presentation at the joint meeting of ICBP Asian section and east Asian bird protection conference, 1989. Bangkok, Thailand.
- POONSWAD, P. & A. TSUJI (1994): Ranges of the males of the Great Hornbill Buceros bicornis, Brown Hornbill Ptilolaemus tickelli and Wreathed Hornbill Rhyticeros undulatus in Khao Yai National Park, Thailand. Ibis 136:79-86.
- POONSWAD, P., A. TSUJI, R. LIEWVIRIYAKIT & N. JIRAWATKAVI (1988): Effects of external factors on hornbill breeding and population. World Conference on breeding endangered species in captivity, Cincinatti, Ohio.
- REDDY, M. S., K. S. MURALIDHAR, M. R. GANDHI & S. BASALINGAPPA (1990): Distribution and variation in number of Malabar Pied Hornbills Anthracoceros coronatus (Boddaert) in selected areas of north Kanara forest of Western Ghats in Karnataka (India). The Indian Zoologist 14:63-73.
- REDDY, M. S. & S. BASALINGAPPA (1995): The food of Malabar Pied Hornbill. Jour. Ecol. Soc. 8:23-28.
- SEIGEL, S. & N. J. CASTELLAN, Jr., (1988): Non-parametric Statistics for the behavioural sciences. McGraw-Hill, New York. 399 pp.
- SNOW, D. (1981): Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13: 1-14.
- TSUJI, A. (1996): Hornbills: Masters of tropical forests, Hornbill Research Foundation, Bangkok
- WELTY, J. C. (1982): The Life of Birds. 3rd edn. Saunders College Publishing
- WHITNEY, K.D., M.K. FOGIEL, A.M. LAMPERTI, K.M. HOLBROOK, D.J. STAUFFER, B.D. HARDESTY, V.T. PARKER & T.B. SMITH (1998): Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon J. Trop. Ecol. 14: 351-371